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OSTEOGRAPHY OF THE EAR REGION IN MONOTREMES

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The ear region in monotremes is decidedly different from that in any other animal, and in some respects it seems to retain reptilian peculiarities otherwise unknown among recent mammals. For both these reasons it has been studied long and often and already has an extensive literature. Most of these publications have a special point of view, considering the ear region embryologically, or cursorily in a review of the whole skull, or incidental to a special consideration of one part, such as the tympanic. Among these many studies, however, there seems to be none that gives adequate descriptions and figures from the point of view most desirable to the comparative osteologist, or to the paleontologist in that capacity. This inadequacy of available data, which certainly is not confined to monotremes since clear and complete osteographic descriptions of the whole ear region of any animal are extremely few, was particularly felt in the course of a recent attempt to interpret the ear region in a multituberculate. This necessitated a rather detailed study of what should strictly be called the osteography of the ear region in monotremes, and the result is here presented. The aim is to illustrate and to identify all the essential structures of the bones surrounding and enclosing the auditory apparatus, as they are seen in macerated skulls of adult monotremes. The tympanic and the auditory ossicles are not discussed, nor are sutures and questions of bone homologies.

Most of these structures have been at least mentioned by one author or another, and the task is thus one of combining and illustrating their results, deciding between conflicting observations, and adding the points that seem to have been omitted. The most important previous work touching the particular subject of this paper is that of Eschweiler, Denker, Van Bemmelen, Van Kampen, Alexander, Gaupp, and Watson (see references). All these authorities have been consulted for data here assembled, but it may be noted that Gaupp's study was found the clearest, most accurate, and most nearly complete from the present point of view. There are a few other contributions, most of them cited by the authors already mentioned, but in general they are of less value for the particular subject of this study, and one or two are merely curiosities.

The material for this study is in the Department of Comparative Anatomy of this Museum and was kindly placed at my disposal by Dr. W. K. Gregory. The illustrations were drawn by John C. Germann.

TACHYGLOSSUS

The Tachyglossidae (or "Echidnidae"[1]) are here represented by specimens of *Tachyglossus aculeatus*, the common (or only) living Australian species of the family.

The outer ear in monotremes has no appreciable effect on the hard parts. There is no bony meatus or even an auditory notch or groove, and the tympanic is free of the cranium and not supported on definite pedicles. The middle ear is widely open below (here and throughout, only the bony structure of a macerated skull is in question) but in *Tachyglossus* is sharply bounded by an elevated and in places underhanging rim. The tympanic cavity as a whole is large and irregularly triangular. The posterior border is almost transverse, only a little more posterior at the external corner, and is formed by ossification of the pars cochlearis capsulae auditivae overlaid by cancellous bone (Gaupp).[2] The inner border of the tympanic cavity is approximately anteroposterior, with the anterior end more external, and is strongly underhung by the so-called echidna pterygoid or epipterygoid (Watson). The third, anteroexternal, border is markedly oblique, anterointernal-posteroexternal, and in its anterior part is defined by a sharp but only slightly underhanging crest against the glenoid surface. The posterior part is complex as will appear below.

A low, well-defined anteroexternal-posterointernal crest immediately anterointernal to the fenestra vestibuli, identified by Gaupp as a crista infrafacialis, divides the roof of the cavity into a large main portion, the fossa tympanica (*sensu stricto*), and a smaller, more complex external and posteroexternal part. The main fossa is simple and in general faces ventrally and slightly externally. The more external part is distinctly concave, while the internal part has an involute but more nearly plane surface. At the most anterior point of the fossa, hidden by the external corner of the epipterygoid when viewed straight from the ventral aspect, is a foramen and canal, fissura petropterygoidea (Gaupp), leading for-

[1] The name *Echinda* is certainly invalid and the personal determination of any zoölogist, however eminent, does not make it any less so. It will perhaps survive as a semi-popular name for an animal of which the correct taxonomic name is not generally familiar and the older popular names are grossly misleading. Zeuglodon, eohippus, dinosaur, ameba, mastodon, and other names show that a scientific term once impressed on the laiety by popularization may acquire a vernacular currency which survives, often usefully, despite the scientific invalidity of the word.

[2] Van Bemmelen identifies this as the mastoid process, but it is clearly not homologous with his supposed mastoid process in *Ornithorhynchus* (see below) and in neither case is it fully homologous with the mastoid process usually so-called in other mammals.

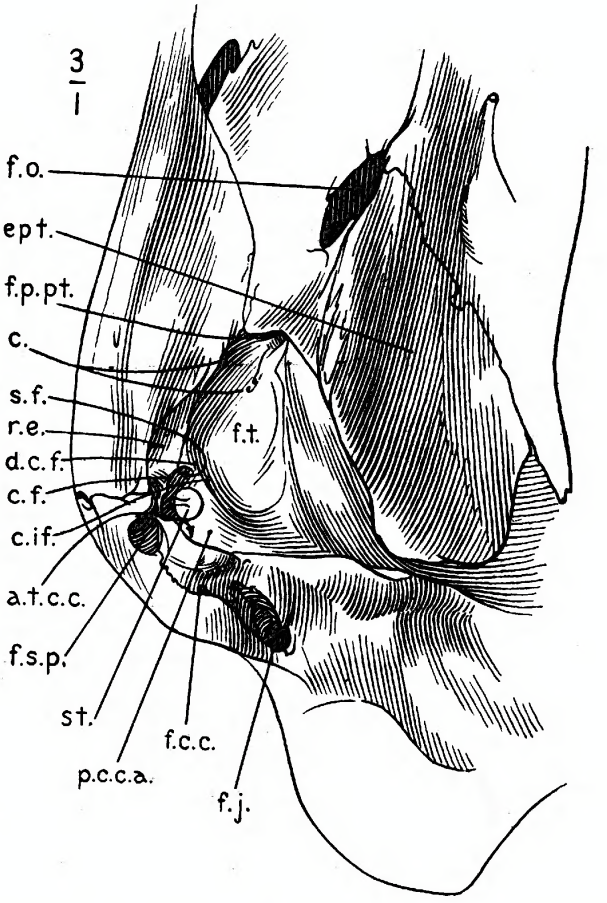

Fig. 1. *Tachyglossus aculeatus.* Ventral view of right side of cranium. Three times natural size.

a.t.c.c., sulcus facialis.
c., dubious canals mentioned on p. 4.
c.f., crista facialis.
c.if., crista infrafacialis.
d.c.f., dehiscentia canalis Fallopii.
ept., epipterygoid.
f.c.c., foramen into canalis craniotympanalis.
f.j., foramen jugulare.
f.o., foramen ovale.
f.p.pt., fissura petropterygoidea.
f.s.p., foramen stylomastoideum primitivum.
f.t., fossa tympanica.
p.c.c.a., pars cochlearis capsulae auditivae.
r.e., recessus epitympanicus.
s.f., apertura tympanica canalis facialis.
st., stapes (in fenestra vestibuli).

ward into the cerebral cavity immediately posterior to the foramen ovale (or pseudovale, Gaupp). External and somewhat posterior to this there are two small foramina opening forward and with shallow grooves leading toward the fissura petropterygoidea. These Gaupp supposed to be for the nervus petrosus superficialis major and the n. p. s. minor, but this can hardly be correct, since at least the more lateral, larger, and more constant of these comes not from the canalis Fallopii but from the canalis proöticus of Gaupp, which would seem to be an impossible course for this nerve.[1]

The posterointernal angle of the tympanic fossa is produced into a deep funnel-like pocket, floored by the epipterygoid, at the end of which is an opening onto the outer surface of the basicranium, near the edge of the basioccipital at the posterior end of the (secondary) palate. This suggests a tuba Eustachii ossea, and has been so identified, but apparently this is incorrect and the canal is vascular. The tuba does indeed depart from this corner of the cavity (and not anteriorly as in other mammals) but is not marked on the bone surface (Eschweiler, Denker). Near the external corner of this main fossa, on the anterior slope of the crista infrafacialis, anterior to the fenestra vestibuli, may appear an oval vacuity, dehiscentia canalis Fallopii (Denker, Van Bemmelen), into the canalis facialis (s. Fallopii), but on my material this is highly variable and may be a mere notch on the crista infrafacialis.

Posteroexternal to the main fossa is a smaller triangular surface, directed outward and downward, in which is the nearly circular fenestra vestibularis. Posterior to this there is a large opening, leading upward, backward, and inward into a large pit or canal with complex features, described below. The opening is the apertura tympanica canalis craniotympanalis (Denker, Van Bemmelen). Externally the surface passes without definite delimitation, except near the anterior end where there may be a low crest, into a broad, curved groove, the sulcus facialis, which carries not only the facial nerve but also a large vein, the vena capitis lateralis. This groove describes an arc of about 90°, the anterior end anteroexternal and the posterior end posteroexternal to the fenestra vestibuli, the posterior end being almost directly posterior to the anterior

[1] Watson (1916, p. 340) says that "ramus palatinus [i.e. nervus petrosus superficialis major] runs forward through a hiatus Fallopii, which forms a canal of variable length. It sometimes stretches to the extreme anterointernal corner of the bone." In Pl. XXIV, fig. 3, he labels a "groove and foramen for the great superficial petrosal nerve." The foramen so labeled seems to be the fissura petropterygoidea of Gaupp, which of course cannot be considered a hiatus Fallopii, as it has no direct connection with the canalis Fallopii. The nervus petrosus superficialis major may have left the canal through the so-called dehiscentia canalis Fallopii (see below) but even in this case the latter is very different in position and relationships from a true hiatus Fallopii, such as occurs in *Ornithorhynchus*, and this hiatus seems to be absent as such or very atypical in *Tachyglossus*.

end and somewhat below the latter. The groove is open into the general tympanic cavity on the internal[1] side, and its floor is formed by a thin, sharp lamella of bone, the crista facialis (s. parotica).

Immediately anterior to the point where the rostral end of the sul-

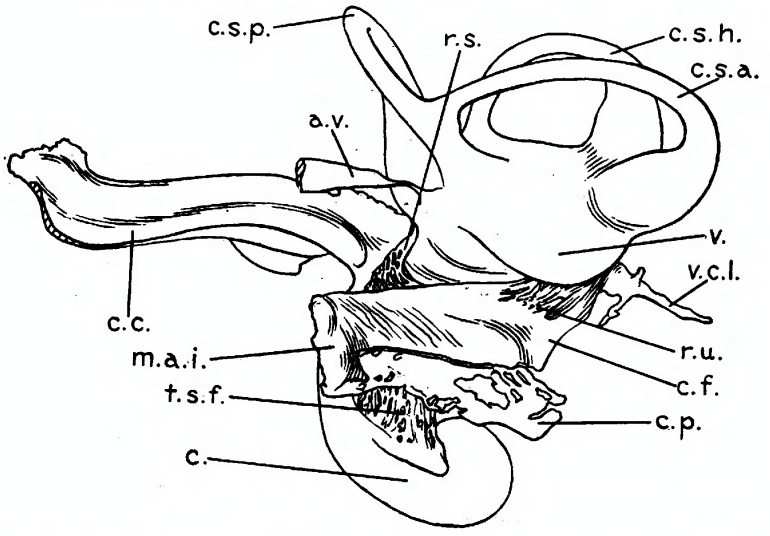

Fig. 2. *Tachyglossus aculeatus.* Internal mold of the inner and part of the middle ear of the left side. Superointernal view. Not to scale. After Denker.

a.v., aqueductus vestibuli.
c., cochlea.
c.c., canalis craniotympanalis.
c.f., canalis facialis.
c.p., pneumatic cells.
c.s.a., anterior semicircular canal.
c.s.h., horizontal semicircular canal.
c.s.p., posterior semicircular canal.
m.a.i., meatus acusticus internus.
r.s., ramus sacculi (of auditory nerve).
r.u., ramus utriculi (of auditory nerve).
t.s.f., tractus spiralis foraminulentus (of auditory nerve).
v., vestibule.
v.c.l., vena capitis lateralis.

cus facialis becomes a closed canal, it divides into two canals. The more medial, somewhat smaller opening, leading into a canal passing medially, is the apertura tympanica canalis facialis.[2] The more lateral and somewhat larger opening leads into a canal that at first passes anteriorly and

[1] It has been customary to describe the monotreme ear as if it were tilted at 90° or somewhat less, so as to orient it more or less like the ears of higher mammals, lateral rather than ventral in the braincase. In such an orientation, this would be the ventral side. This convention seems to me to lead to endless confusion, and I have throughout described the ear as it is, not as it might be if it conformed with some fictitious rule.

[2] This term has been applied to the slightly more posterior tympanic aperture of both canals after their union, or the two have not been sharply distinguished. The distinction does not seem very important, but strictly this is the actual end of the facial canal as such and the short common canal for nerve and vessels is distinct.

somewhat medially, then turns dorsally, somewhat laterally, and finally posteriorly and then opens into the cranial cavity where the sulcus sinus transversi leads into it. This canal transmits the vena capitis lateralis

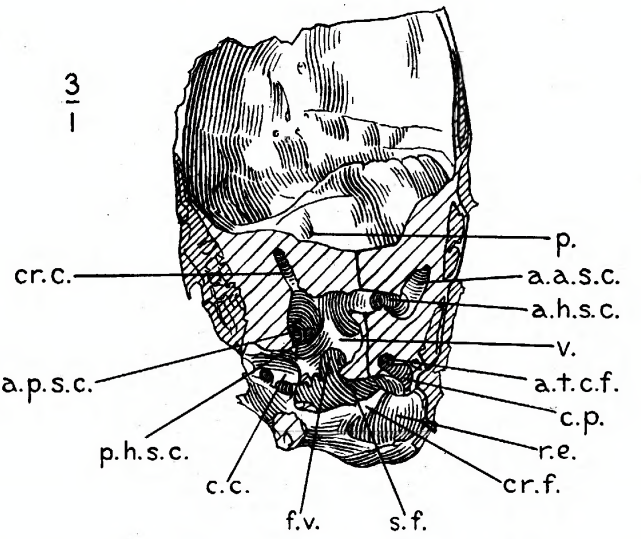

Fig. 3. *Tachyglossus aculeatus.* Skull fragment from the left side, removed by two vertical cuts, one directly anteroposterior and one directly transverse, meeting at the anterointernal corner of the vestibule. The view is almost directly posteroexternal, the cross-lined part to the left being the anteroposterior and that to the right the transverse cut. Above this is the endocranium, in it the inner ear, and below it the middle ear. Three times natural size.

a.a.s.c., recess for ampulla of anterior semicircular canal.
a.h.s.c., recess for ampulla of horizontal semicircular canal.
a.p.s.c., recess for ampulla of posterior semicircular canal.
a.t.c.f., apertura tympanica canalis facialis.
c.c., canalis craniotympanalis.
c.p., canalis proöticus.
cr.c., canal for crus commune.
cr.f., crista facialis.
f.v., fenestra vestibuli.
p., small pit in endocranial aspect of periotic.
p.h.s.c., posterior vestibular aperture of horizontal semicircular canal.
r.e., recessus epitympanicus.
s.f., sulcus facialis.
v., vestibule.

and is called the canalis proöticus by Gaupp. The intracranial opening is called the foramen vasculosum internum by Van Bemmelen.

At its posterior end the sulcus facialis turns ventrally and enters an opening lateral to the previously mentioned apertura tympanica canalis

craniotympanalis. After passing through a very short canal, hardly worthy of separate designation as such, the passage issues through a circular opening on the base of the skull, approximately at its posteroexternal angle. This is the foramen stylomastoideum (or more accurately the f. s. primitivum; a foramen stylomastoideum, foramen faciale, or foramen stylomastoideum definitivum in the sense of Van Kampen is not formed in monotremes).

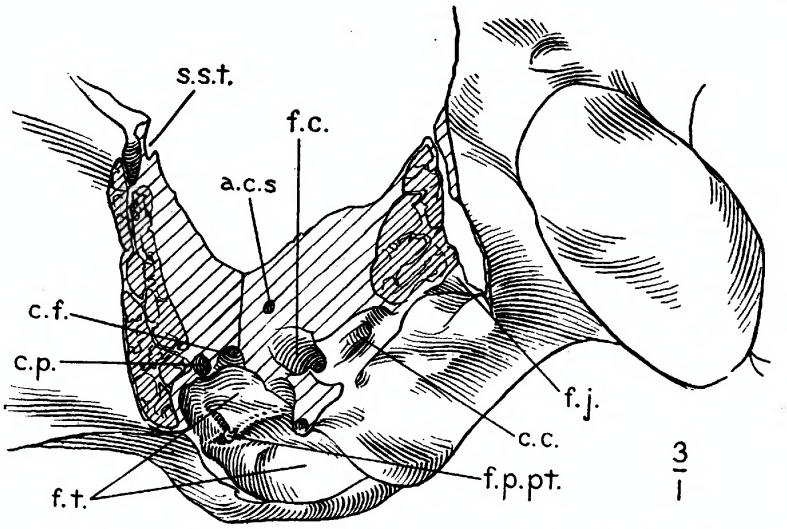

Fig. 4. *Tachyglossus aculeatus.* The sectioned specimen of Fig. 3, showing the skull from which the piece seen in Fig. 3 was cut, looking anterointernally. Three times natural size.

a.c.s., area cribrosa superior.
c.c., canalis craniotympanalis.
c.f., canalis facialis.
c.p., canalis proöticus.
f.c., fossa cochleae.
f.j., foramen jugulare.
f.p.pt., fissura petropterygoidea.
f.t., fossa tympanica.
s.s.t., sulcus sinus transversi.

Ventral to the sulcus facialis is another sulcus or pocket, also open on the medial side. The roof is formed by the crista facialis posteriorly and by a process of the squamosal anteriorly. The floor is less extensive and is formed mainly by an inflection of the squamosal, met posteriorly by a periotic process from the region of the foramen stylomastoideum. This pocket is the recessus epitympanicus (Van Kampen, Gaupp, etc.; the term has also been less correctly used to include a larger part of the tympanic cavity).

The region dorsal and posterior to those already described includes a complex of cavities to which in general the name canalis craniotympanalis was applied by Denker. Gaupp pointed out that this included the foramen jugulare, which is properly a thing apart, and confined the name canalis craniotympanalis to the opening leading from the tympanic cavity. There does not appear to be any clear description of the details of this region, details which are, indeed, variable but still include characteristic features. The opening already mentioned under the name apertura tympanica canalis craniotympanalis leads into an irregular cavity,

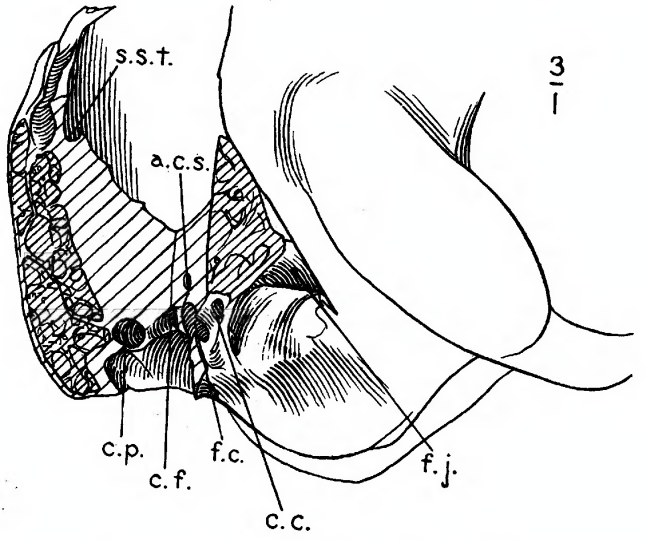

Fig. 5. Same as Fig. 4, looking anteriorly.

a.c.s., area cribrosa superior.
c.c., canalis craniotympanalis.
c.f., canalis facialis.
c.p., canalis proöticus.
f.c., fossa cochleae.
f.j., foramen jugulare.
s.s.t., sulcus sinus transversi.

not in itself really canal-like. The antero-superointernal edge of the aperture is a well-defined crest, posterointernal to the fenestra vestibuli and above this is a pocket in the bottom of which is an oval aperture, facing postero-inferolaterally, the fenestra cochleae. External and posterior to this there is a rounded expansion of the chamber, with several variable foramina opening into the diploe of the adjacent cancellous bone. Posteriorly and dorsally the cavity narrows somewhat into a canal which opens into the jugular canal near its lower (extracranial)

end. This often has one or two small foramina into the diploe in its walls. The extent to which it is roofed over varies, but there seems rather constantly to be a hiatus in the posterior wall, so that the canal also has an opening distinct from and anteroexternal (and ventral) to the foramen jugulare. There is also a distinct and smaller canal, beginning on the antero-superomedial wall of the main canal, paralleling the latter in a

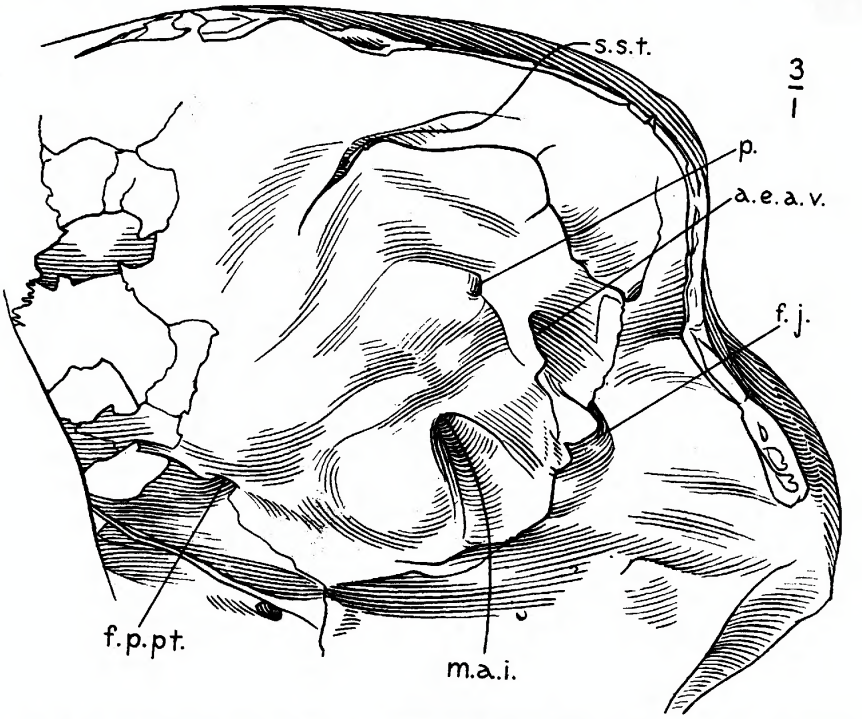

Fig. 6. *Tachyglossus aculeatus.* The endocranial aspect of the right ear region of a skull with the roof cut away. Superointernal view. Three times natural size.

a.e.a.v., endocranial aperture of aqueductus vestibuli.
f.j., foramen jugulare.
f.p.pt., fissura petropterygoidea.
m.a.i., internal auditory meatus.
p., pit in endocranial aspect of periotic.
s.s.t., sulcus sinus transversi.

dorso-posteromedial direction, and opening separately into the inner part of the jugular canal. The point of opening varies considerably and in some cases is so far intracranial that it is clearly distinguishable from the jugular canal in an endocranial view and can hardly be said to open into the latter canal, with which it is, nevertheless, closely associated and into which it usually seems to open.

The internal ear has been well described by Denker, who treats the bony labyrinth of the adult, and by Alexander, who deals with the embryology and histology of the soft tissues, not part of the present subject but useful in interpreting the osteology. Denker figures and describes molds of the cavities, made by filling them with molten metal and then etching away the bone. I here supplement these data by figures of a dissection made by two vertical saw-cuts on the macerated skull, such as to reveal most of the important internal features. In view of the general adequacy of the previous work and clarity of the figures available, not much detail is necessary.

The vestibule proper, or its central portion, is somewhat distinct from a deep posteroexternal pocket, with the opening of the crus commune in its roof, near its (vaguely defined) mouth, and the opening and space for the ampulla of the posterior semicircular canal in its posteroinferior part and the posterior opening of the horizontal canal immediately anteroexternal to this. A similar anteroexternal recess has the large cavity for the ampulla of the horizontal semicircular canal in its outer part, and above and, for the most part, slightly anteromedial to this is the less pronounced fossa for the ampulla of the anterior semicircular canal. On the medial side the vestibule gradually narrows and passes into the large, curved fossa cochleae. As is well known this fossa (in all monotremes) is unique among recent mammals in being nearly uncoiled. That is, it does not complete one whole turn, but it is, nevertheless, spiral. It is more transverse than anteroposterior.

The aqueductus vestibuli (for the ductus endolymphaticus) opens into the roof of the vestibule between the outer end of the fossa cochleae and the opening of the crus commune. Hence the aqueduct, which is very small, runs upward, backward, and inward to its opening on the endocranial aspect of the periotic.

The inner surface of the periotic is rather simple and there is no fossa subarcuata, in sharp distinction from *Ornithorhynchus* and most primitive mammals. The porus acusticus internus is near its posteromedial corner and opens into a true meatus running forward and outward and, in its most lateral part, also upward. This most lateral and somewhat dorsal portion has the beginning of the canalis Fallopii anteriorly, and posterior to this is the area (s. macula) cribrosa superior (or foramen acusticum superius—seen as a foramen in the dissection but cribriform when uncut—)the ducts from which open into the upper part of the medial wall of the vestibule and carry the ramus utricularis (Denker) or nervus utriculo-ampullarus (Alexander, Gaupp). Below these, the mea-

tus is expanded into a pocket which lies parallel to and above the fossa cochleae. In the floor of this are many fine ducts, for the nerve to the cochlea, forming the area cribrosa anterior (Alexander, Gaupp) or tractus spiralis foraminulentus (Denker—this is indeed the homologue of the tractus spiralis, but in monotremes it is not spiral), the successor of a more united foramen acusticum inferius in young animals (Gaupp). At the posterolateral end of this expansion of the meatus is the macula cribrosa inferior (Alexander), successor of the foramen acusticum medium (Gaupp), through which the posterior ampulla and probably also the sacculus are innervated.[1] In my material, and in the various illustrations available, this macula is not very sharply distinguishable from the area cribrosa anterior.

Near the posterior edge of the endocranial surface of the periotic and postero-superolateral to the porus acusticus internus, is an irregular superolateral-inferomedial slit, the apertura externa aqueducti vestibuli, which passes forward into the bone and narrows rapidly to form the minute aqueductus vestibuli. Antero-superolateral to this, and superolateral to the porus, there is sometimes, but not invariably, a small pit, which does not appear to be a foramen or other functional structure. The sulcus sinus transversi is well marked in its curved course leading into the canalis proöticus, already described. Starting at the posterior end of its course is a distinct sulcus and extending postero-inferomedially to the suture with the occipital is a well marked groove or elongate pit. At the edge of the periotic posterior to the porus is the endocranial end of the foramen jugulare (plus the foramen condyloideum, which is not separate in monotremes, and also plus the canalis craniotympanalis) and in an analogous position at the antero-inferomedial border of the periotic is the endrocranial opening of the fissura petropterygoidea.

ORNITHORHYNCHUS

The Ornithorhynchidae are represented by several specimens, juvenile to senile, of the typical *Ornithorhynchus anatinus*, generally considered to be the only living species of the family although others have been proposed. At first sight the ear region in this animal appears to be basically unlike that of *Tachyglossus*, but in fact the structural resemblance proves to be close. Most of the differences are superficial and are dependent on proportions, degree of ossification of various regions, and other features that overlie but do not conceal fundamental agreement such as is consonant with community of origin.

[1] The various accounts do not seem to be consistent as to the exact distribution of nerves through this area, and the problem cannot be solved osteologically.

The tympanic cavity (and indeed the ear region as a whole) is much smaller relative to the rest of the skull in *Ornithorhynchus* than in *Tachyglossus* and is also rendered less definite and conspicuous by the absence of any elevated rim or other sharp boundary on the medial, anterior, or posterior sides. There is, however, a strong underlapping lamina on the lateral side which is also produced backward as a projection beyond the ear region proper. This is the processus mastoideus of Van Bemmelen, but later revision (Gaupp, Watson, etc.) suggests that this structure as a whole is to be considered as a crista parotica. The medial margin of the anterior part has a large semicircular incisure, above the middle of which is the fenestra vestibuli. The posterior margin of this incisure is formed by a small but stout process directed almost straight medially, at a lower level than the roof of the tympanic recess. This is the processus hyoideus of Van Bemmelen (formed by a tympanohyal according to Van Kampen). Although (on the macerated skull) a gap is left between its inner end and the body of the periotic, it is homologous with the bridge of bone enclosing the foramen stylomastoideum primitivum ventrally in *Tachyglossus*. The medial rim of the incisure and anterior rim of the processus hyoideus are thick and vaguely and slightly excavated. This is suggestive of the much more obvious and larger recessus epitympanicus of *Tachyglossus*, but that recess is not otherwise present and indeed is best recorded, as is usually done, as quite absent as such in *Ornithorhynchus*.[1]

Above the crista parotica, lateral to the fenestra vestibuli, is the large curving sulcus facialis, as in *Tachyglossus*, and, also as in that genus, it is evidently more extensively occupied by blood vessels than by the actual facial nerve. The lateral part of the anterior end leads into a canalis proöticus, quite as in *Tachyglossus*, and there is also a smaller branch that runs anterolaterally and opens on the external surface of the skull, immediately anteromedial to the glenoid fossa, as the foramen vasculosum externum laterale (Van Bemmelen), which Watson states to be for the arteria temporalis superficialis. Medial and somewhat anterior to this is the apertura tympanica canalis facialis. The canalis facialis (s. Fallopii) curves forward, upward, and then backward from this foramen to the internal auditory meatus. Immediately anterior to the periotic in this region is a great opening, larger than in *Tachyglossus*, the foramen pseudovale (including in its functions that of the foramen

[1] This is clearly brought out by Van Kampen and Gaupp and accepted by most later students, but earlier writers usually did not clearly distinguish between the recessus epitympanicus and the groove called the sulcus facialis by Van Kampen and most subsequent workers, and this confusion is still occasionally encountered.

ovale s. s.), within the rim of which, at its posteroexternal end, is a pronounced recess on the anterior side of the anterolateral part of the strictly auditory region of the periotic. In the posterior wall of this recess there is a marked hiatus in the facial canal (hiatus canalis Fallopii, Denker,

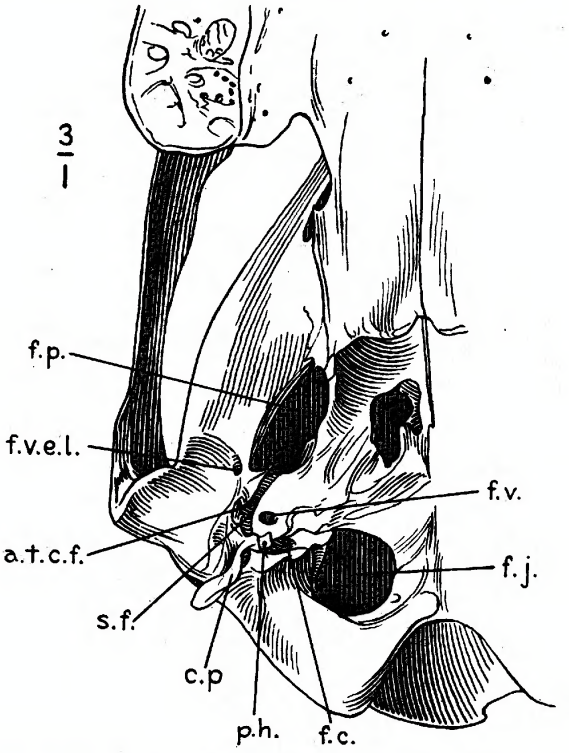

Fig. 7. *Ornithorhynchus anatinus.* Right part of the basicranium, seen from below and somewhat internally. Three times natural size.

a.t.c.f., apertura tympanica canalis facialis.
c.p., crista parotica.
f.c., fenestra cochleae.
f.j., foramen jugulare.
f.p., foramen pseudovale.
f.v., fenestra vestibuli.
f.v.e.l., foramen vasculosum externum laterale.
p.h., processus hyoideus.
s.f., sulcus facialis.

etc.), which thus is open anteriorly in about the middle of its course from the internal auditory meatus to its tympanic aperture. The position of this hiatus is different from that of the dehiscentia canalis Fallopii of *Tachyglossus*, which it may otherwise resemble, for the latter is within the tympanic cavity.

The nearly closed notch above the processus hyoideus is evidently homologous with the foramen stylomastoideum primitivum in its lateral part and with the apertura tympanica canalis craniotympanalis of *Tachyglossus* in its medial part, although in *Ornithorhynchus* the two are not separated from each other by a bridge of bone and the two together are not entirely enclosed by bone. They are, however, divided by a small sharp nearly anteroposterior ridge (slightly more medial anteriorly) in the roof of the common passage. There is a pit dorsal and posterior to what I consider as structurally the a. tymp. can. craniotympanalis, and the fenestra cochleae opens posteriorly into this. An open groove runs internally from the pit into the great vacuity which includes the foramen jugulare; compare in *Tachyglossus* the more enclosed and more posterior but structurally similar connection.

The bony labyrinth has been fully described by Denker. It is similar to that of *Tachyglossus* and offers so few peculiarities that no additional description seems necessary.

The endocranial aspect of the ear region is sharply distinguished from that of *Tachyglossus* by the development of a pronounced shelf with a sharp (medial) rim below the sulcus sinus transversi and of an unusually large and deep fossa subarcuata, the mouth of which is approximately triangular. The anterior semicircular canal runs within its anterosuperior rim and the crus commune within the likewise sharp posterior rim. In the anterior wall of the fossa there is a short canal into the sinus sulcus transversi, near the endocranial end of the canalis prooticus. The apertura externa aqueducti vestibuli is a small opening, not enlarged or slit-like as in *Tachyglossus*, on the eminence below the inferomedial angle of the rim of the fossa subarcuata. The porus acusticus internus is a pit, without a definite meatus as in *Tachyglossus*, anteroinferomedial to the fossa subarcuata and considerably smaller than the latter.

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